

SUPRASPECIFIC CLASSIFICATION IN THE SCROPHULARIACEAE: A REVIEW

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The present status of our knowledge of the classification of the Scrophulariaceae, a family of perhaps 250 genera and 5000 species (Thieret, 1959), reflects the general lack of detailed information regarding intra- and extra-familial relationships of many of the families of flowering plants. New and detailed research on the family, using whatever tools are available, and a re-evaluation of past research are necessary before a logical taxonomic treatment of the family can be realized. The necessity of such research and such re-evaluation is attested to by the essentially pre-evolutionary, century-old treatment of the family found in the majority of the world's floras. The present paper is meant as a summary of major taxonomic problems presented by the Scrophulariaceae and of especially significant past taxonomic research that has been carried out on the supra-specific level in the family.

My interest in the family was awakened a number of years ago when I began a study of gross internal and external morphology of scrophulariaceous seeds in relation to supra-specific classification of the family. It soon became evident that the taxonomy of this family is in a sorry state indeed, as the following pages will show.

Wettstein (1935) briefly but pointedly characterized the current state of the classification of the Scrophulariaceae when he wrote (p. 897): "Eine natürliche Systematik innerhalb der Familie ist zur Zeit noch nicht erreicht." Indeed, even the limits of the family itself are not agreed upon (compare, for example, the treatments of Wettstein, 1891, and Hallier, 1903).

PREVIOUS CLASSIFICATIONS

The treatment of the Scrophulariaceae which is generally accepted today is that formulated by Wettstein (1891). This, in turn, is based upon the earlier revisions of Bentham and Hooker (1876) and Bentham (1846). The work of Bentham is the latest one to give an account of all the (then-known) species of the family. This revision, now 121 years old, takes little or no account, of course, of the phylogeny of the Scrophulariaceae. The two subsequent revisions (each on a generic basis) left Bentham's work basically unchanged. Consequently, most treatments of the family (or portions of it) in print today are merely reiterations of a pre-evolutionary, century-old system. Yet, as Pennell (1935) pointed out, the Scrophulariaceae are a family which may be presented on a "remarkably developmental basis."

Additions to and some minor revisions of Wettstein's treatment of the Scrophulariaceae have been published in *Die Natürlichen Pflanzenfamilien Nachträge* (Diels, 1908, 1914; Wettstein, 1897). In *Das Pflanzenreich* only the Calceolarieae have appeared (Kränzlin, 1907).

A revision of Wettstein's treatment of the Scrophulariaceae was published in 1903 by Hallier (1903). The most significant features of the revision include the abandonment of characteristics of aestivation as the basis for defining subfamilial divisions; the enlargement of the family to include the Plantaginaceae, Lentibulariaceae (see Mez, 1936), and Orobanchaceae; and the tribal reassignment of many genera. Unfortunately, as Diels (1908) pointed out: "Eine streng analytische Begrenzung der vorgeschlagenen Triben ist nicht gegeben; sie dürfte sich auch schwer schaffen lassen." Hallier's discussion of the systematic position of the Selagineae and *Lagotis* is doubtless the most detailed and critical one given to date. He accepted the inclusion of the Selagineae in the Scrophulariaceae and the removal of *Lagotis* from this tribe to the Digitaleae although in a previous paper (Hallier, 1901) he felt that Baillon and Wettstein were wrong in making these assignments. Of Hallier's revision of the family, Diels (1908) wrote: "Da er, abgesehen von eigenen Anregungen, viele schon früher geäußerte Gedanken zusammenstellt und verwertet, sei sein System als Material für weitere systematische Arbeit an der Familie mitgeteilt."

A provocative primary division of the family, based upon staminal characteristics, was proposed by Van Tieghem (1903). Two types of stamens, differentiated by their anthers, were distinguished, as follows: (a) tétrathèque ("Dorsifixe, pendante, bifide et creusée de quatre sacs polliniques longitudinaux") and (b) dithèque ("basifixe, dressée, entière et creusée seulement de deux sacs polliniques transversaux"). According to Van Tieghem, the latter can be derived from the former by atrophy of one half of the anther and displacement of the remaining half which, now median and transverse, becomes bent at the summit of the filament.

The tetrathecal type is found in that division of the family which Van Tieghem called "*Holantherées*," and the dithecal type in the "*Hémianthérées*." Representative holantherous genera are *Anthirrhinum*, *Linaria*, *Mimulus*, *Paulownia*, *Rhinanthus*, and *Melampyrum*. Genera of the hemiantherous division include *Scrophularia*, *Verbescum*, *Celsia*, *Chaenostoma*, *Manulea*, *Nemesia*, and *Limosella*. Among the holantherous genera are certain ones (*Harveya*, *Sopubia*, *Centranthera*, *Cycnium*, *Striga*, *Zaluzianskia*, and *Buchnera*) in which one-half of the anther is more or less aborted but not displaced. In Van Tieghem's opinion these genera form a link between the *Holantherées* and *Hémianthérées*.

After a study of the characteristics of the nectary of a number of genera of the Personatae (i.e., Scrophulariaceae), Bellini (1907) proposed a classification of the family based principally upon these characteristics.

According to him, it is possible to distinguish, with regard to the nectary, four types of Personatae, as follows: (a) nectary is situated upon the hypogynous disc or in a "*glandola antica*," (b) nectary originates from the aborted fifth stamen, (c) nectary originates from the bases of the filaments of the larger stamens, and (d) nectary is petaloid or lacking.

The Personatae were divided by Bellini into two sub-families, the Scrophulariaceae (not parasitic) and the Rhinanthaceae (parasitic or semi-parasitic). The Rhinanthaceae were further characterized by the development of the nectary in a "*glandola antica*," a condition unknown in the other subfamily. Otherwise, nectary characteristics were not used in the Rhinanthaceae, the tribes of this subfamily (Gerardieae, Pedicularineae, and Orobanchaeae) being equivalent to the Gerardieae and Rhinanthaeae of Wettstein (1891) and the Orobanchaceae.

In the subfamily Scrophulariaceae, tribal divisions were based primarily upon nectary characteristics. Some of the tribes recognized by Bellini (Verbasceae, Hemimerideae, and Calceolarieae) are equivalent to these tribes as delimited by Wettstein. On the other hand, Wettstein's Antirrhineae were divided into the Linarieae (with calcarate "*nettaroconca*") and Antirrhineae (with saccate "*nettaroconca*"). In contrast to these homogeneous tribes, others, as delimited by Bellini, are heterogeneous groups of genera, e.g., the Mimuleae (including *Mimulus*, *Paulownia*, and *Maurandya*) and the Digitaleae (including *Digitalis*, *Scrophularia*, *Ghiesbreghtia* (= *Eremogeton*), and *Lindernia*). These tribes, though possessing nectarial homogeneity, are composed of genera which, by virtue of a host of other characteristics, are discordant in such close alliance.

The genera *Collinsia* and *Tonella* were placed by Bellini in the tribe Collinsieae (here first proposed), a taxon characterized by the origin of the nectary from the aborted fifth stamen. This recognition of the distinctness of the Collinsieae is one of the salient features of Bellini's classification. Unfortunately, it was overlooked by Pennell (1935) who "proposed" the identical taxon Collinsieae based, however, on characteristics other than those of the nectary.

The Orobanchaceae have been included in the Scrophulariaceae not only by Bellini but also by Hallier (1903). It has long been recognized that certain members of both taxa are essentially alike in habitat, habit, flower structure, and seed-coat structure (Tiagi, 1952). Both are characterized by the formation of endosperm haustoria (Glisic, 1929). According to Boeshore (1920), the two taxa are alike logically and biologically and thus should be treated in "continuous descending series from the highest to the most degraded genera." (See also Linsbauer and Ziegenspeck, 1943).

The conspectus of the tribes and genera of the Scrophulariaceae published by Rouy (1909) is essentially a combination of various features

of the Bentham, Bentham and Hooker, and Wettstein treatments of the family.

Some attempts at a reclassification of certain portions of the family on a phylogenetic basis were made by Pennell (1935). Pennell's work in the Scrophulariaceae, however, was confined almost entirely to the New World (and North America in particular). Thus, his reclassification was based upon his extensive knowledge of the New World representatives of the family and, as a result, does not take into consideration the numerous Old World representatives. Treatments of the Scrophulariaceae based upon Pennell's work have appeared, of course, in his papers of a floristic nature (1919, 1920, 1921, 1923, 1935, 1941) and in at least two floras, both of them of areas in North America (Abrams, 1951; Gleason, 1952). Pennell's contributions to a phylogenetic classification of the Scrophulariaceae, though of inestimable value, must be regarded as provisional until a world-wide study of the family is made with a view to reclassification.

SUBFAMILIAL DIVISIONS

In Wettstein's (1891) treatment of the Scrophulariaceae, the primary divisions of the family are the Pseudosolaneae, Antirrhinoideae, and Rhinanthoideae. These divisions may be presumed to be subfamilies although they were not designated as such by Wettstein. The Pseudosolaneae have the initial position, apparently to emphasize their supposed affinities with the Solanaceae based upon the nearly actinomorphic corolla, alternate phyllotaxy, and presence of the full complement of five stamens in *Verbascum*. *Verbascum* has long been regarded as the logical connecting link with the Solanaceae and has been considered to be "on the road to acquiring zygomorphism, but to which [it] has [not] yet fully attained" (Henslow, 1893). According to Wettstein (1891), "Am nächsten stehen die Scrophulariaceen den Solanaceen, zu denen der Übergang einerseits durch die Verbasceae, andererseits durch die Salpiglossideae vermittelt wird." Indeed, the Salpiglossideae have even been included in the Scrophulariaceae, as in Bentham's treatment of the family (Bentham, 1846).

Apparently the first person to cast doubt upon the presumed primitiveness (and thus upon the presumed solanaceous affinities) of *Verbascum* was Robertson (1891) who supposed "the prototype of *Verbascum* to have been a bilabiate flower with didynamous stamens, because the type of the order is didynamous and because the two genera with which *Verbascum* form the tribe Verbasceae have only four stamens."

Impressive evidence to refute the presumed affinities of *Verbascum* with the zygomorphic Solanaceae was presented by Robyns (1931) who disclaimed the alliance because the zygomorphy characteristic of *Verbascum* is of the type characteristic of other members of the Scrophulariaceae but not of the zygomorphic Solanaceae. Robyns emphasized most strongly the oblique alignment of the carpels in the Solanaceae as

contrasted with their median alignment in the Scrophulariaceae and the loss or reduction of one of the anterior stamens in many Salpiglossideae as contrasted with the loss or reduction of the posterior stamen in most Scrophulariaceae.

In aestivation the corolla is plicate in the Solanaceae but imbricate in the Scrophulariaceae. Anatomical evidence against the alliance is furnished by the bicollateral vascular bundles of the Solanaceae, whereas those of the Scrophulariaceae are collateral. The *Verbascum* type of seed, characterized by the presence of longitudinal and transverse endosperm ridges and local proliferation of cells in the inner layers of the testa, apparently is not found in the Solanaceae.

Thus, the conclusion may be reached that the long accepted affinity of the Verbasceae with the Solanaceae is apparent rather than real. However, the position of the Verbasceae within the Scrophulariaceae remains an open question, i.e., is the tribe primitive or derived.

Robertson's (1891) conclusion, that the prototype of the flower of *Verbascum* was a bilabiate flower with didynamous stamens, is identical with that reached by Pennell (1935) who regarded the nearly actinomorphic corolla, the frequent presence of five stamens, and the alternate leaves as derived rather than primitive characteristics in the Scrophulariaceae. Further evidence that the Verbasceae are not primitive members of the family may be seen in the united stigmas and the relatively complex seeds of this taxon.

Since the subfamily Pseudosolaneae was based on the supposed affinities of its members with the Solanaceae, and since these affinities have been shown to be unreal, this subfamily should be dissolved (Pennell, 1935). The Scrophulariaceae, then, are divided into two subfamilies, the Antirrhinoideae and the Rhinanthoideae. These differ in the external position of the posterior corolla lobes in aestivation in the former as contrasted with the external position of the anterior corolla lobes in the latter. The Verbasceae, Leucophylleae, and Aptosimeae, the three tribes included in Wettstein's Pseudosolaneae, must now be placed in the Antirrhinoideae.

The relative position of the corolla lobes in aestivation as the basis for dividing the Scrophulariaceae into two subfamilies seems to be a slight difference upon which to found so fundamental a distinction. However, as Pennell (1935) wrote, "it appears to be one of great racial value." Nevertheless, further investigation may disclose other criteria upon which to base the sub-familial division of the Scrophulariaceae. Schmid (1906) questioned the inclusion of *Digitalis* in the same subfamily as the Gerardieae (=Buchnereae) and Rhinanthae (=Euphrasieae) because this genus, in its embryology, has little in common with the two latter taxa, which apparently are embryologically quite similar. The Digitaleae are not root parasites, another point of contrast with the usually parasitic Gerardieae and Rhinanthae. Bellini (1907) used para-

sitism versus non-parasitism as the criterion for the division of the Scrophulariaceae into the two subfamilies. Hallier (1903) did not consider aestivation characteristics as a good basis for the subfamilial division, for he wrote: "Es scheint mir daher natürlicher zu sein, die alte Benthamsche, auf die Art der Knospendeckung der Krone gegründete Eintheilung der Familie ganz fallen zu lassen. . . ." Hartl (1957) reported that the anterior lobes of the corolla of *Lindenbergia*, a genus of the Antirrhinoideae, are external in the bud, which lends credence to Diels' (1897) assertion that the relative position of the corolla lobes in the bud is, in certain cases, a feature of little importance in establishing relationships.

Since the Verbasceae have been shown to possess characteristics which, in the Scrophulariaceae, are derived rather than primitive, this tribe may no longer occupy the initial position in the family. Search for the initial tribe should take place among the Antirrhinoideae since the Rhinanthoideae, on the basis of specialized habits of parasitism and of elaborate zygomorphy, appear to be the derived group.

A survey of the seeds of the Antirrhinoideae reveals that the most simple seeds (structurally) are found almost exclusively in the Gratioleae. Here, then, is a suggestion that this tribe may represent the primitive type of Scrophulariaceae. Additional investigation of the tribe brings forth other evidence which supports this suggestion: usually distinct stigmas, usually septicidal dehiscence of the capsule, usually distinct sepals, the racemose inflorescence, and the opposite phyllotaxy. It seems, then, logical to assign the Gratioleae to the initial position in the family, as has been done by Pennell (1935).

THE TRIBES

The following discussion of certain tribes of the Scrophulariaceae deals with these taxa as delimited by Wettstein (1891) and as usually recognized at present.

VERBASCEAE

The Verbasceae (sensu Wettstein, 1891) comprise five genera: *Verbascum*, *Celsia Staurophragma*, *Leucophyllum*, and *Ghiesbreghtia* (= *Eremogeton*). Presumably a more logical treatment of this taxon would be its division into two tribes, the Verbasceae (sensu Bentham, 1846) and the Leucophylleae (sensu Bentham and Hooker, 1876). That these two taxa are probably closely related is shown by their alternate leaves and, more especially, by their branched trichomes, a feature restricted, in the Scrophulariaceae, to these taxa. However, their many points of difference surely entitle them to tribal (rather than subtribal) rank. The Verbasceae are Old World plants; the Leucophylleae are New World plants. In the Verbasceae the flowers are disposed in simple or compound racemes or spikes and the corolla is rotate; in the Leucophylleae the flowers are axillary and the corolla is campanulate. The anther sacs are

wholly confluent in Verbasceae but distinct in Leucophylleae. At least the posterior filaments in the Verbasceae are villous, whereas all filaments in the Leucophylleae are glabrous. In addition to the above characteristics must be mentioned the seeds of *Verbascum* and *Celsia* (with their characteristic ridges attributable to endosperm proliferation) as contrasted with the scalariform-reticulate seeds of *Eremogeton* and *Leucophyllum*. Indeed, judging from the seeds, *Verbascum* and *Celsia* may be less closely related to the Leucophylleae than to *Scrophularia* and *Russelia*.

CHELONEAE

The Cheloneae, as presented by Bentham (1846) and enlarged by Wettstein (1891), are an assemblage of genera whose principal common characteristic is the cymose disposition of the flowers. As the result of the use of this characteristic as the principal one defining the Cheloneae, including herein all Scrophulariaceae (except Calceolarieae) possessing such inflorescences, this tribe possesses a heterogeneity equalled in the family only by the Digitaleae sensu Wettstein.

An examination of the genera included in the Cheloneae by Wettstein reveals that many of them possess features which show them to be closely related to taxa other than the Cheloneae.

To the Bignoniaceae were transferred *Synapsis* by Urban (1926), *Paulownia* by Campbell (1930), and *Wightia* by Hallier (1903). Hallier transferred *Brookea* and *Uroskinnera* to the Gesneriaceae, the transfer of the latter genus being perhaps in error (Schultes, 1941).

Leucocarpus, *Berendtiella* (= *Berendtia* A. Gray), and *Hemichaena*, as is evidenced by their distinct, plate-like stigmas, their campanulate, 5-ribbed, 5-toothed calyces, and their loculicidal capsules (in the last two genera), are near allies of *Mimulus* and thus must be transferred to the Gratioleae (Pennell, 1935). *Leucocarpus*, even though it possesses a bacate fruit, is obviously closely related to *Hemichaena* as is evidenced not only by its distinctive stigmas and calyx but also by its reticulate seeds with intra-reticular lines of a type apparently found nowhere else in the Scrophulariaceae except in these two genera.

Because of distinctive nectary characteristics of *Collinsia* and the closely related *Tonella*, Bellini (1907) proposed the tribe Collinsieae to include these two genera. Apparently overlooking Bellini's work, Pennell (1935) also proposed a tribe Collinsieae for *Collinsia* and *Tonella*. In addition to the characteristics of the nectary and those mentioned by Pennell (greatly modified "papilionaceous" corollas, loculicidal capsules, and annual duration), the distinctive large seeds, few in number per capsule, and the spatulate embryos provide ample justification for the setting apart of these genera in the Collinsieae.

The genus *Russelia*, recently monographed by Carlson (1957), appears to be somewhat enigmatic in its relationships. The outstanding characteristic of the genus is the presence of densely packed long hairs with-

in the loculicidal capsule. By virtue of this characteristic, which occurs nowhere else in the Scrophulariaceae, *Russelia* seems to be a somewhat isolated genus and may perhaps best be treated as the sole member of the tribe Russelieae. The close resemblance of the seeds of *Russelia* and *Scrophularia* to those of *Verbascum* and *Celsia* suggests a closer relationship between these two groups of genera than is indicated by current classifications.

After the above mentioned genera have been transferred from the Cheloneae sensu Wettstein, the remaining genera form a slightly less heterogeneous taxon but one, nevertheless, which is still discordant. For example, it contains both baccate and capsular fruits, both loculicidal and septicidal capsules, and some of its genera are characterized by the presence of staminodes while others show no trace of the fifth stamen.

Certain problems appear uppermost in an attempt at redefining the Cheloneae; several of these will be briefly discussed here.

What is the taxonomic significance of the baccate fruit of *Dermatocalyx*, *Halleria*, and *Teedia*? To include both baccate and capsular fruits within the same tribe seems somewhat inconsistent. However, both Bureau (1863), in a study of *Monttea*, and Cr  t   (1952), in an embryological study of *Teedia lucida*, recommended that not too much taxonomic importance should be attributed to fruit type in the Scrophulariaceae. An obvious example of the misplacing of a genus as the result of emphasis of fruit type is seen in *Leucocarpus*, formerly included in the Cheloneae among the other genera with baccate fruits, but which must pass to the Gratioleae and stand near *Mimulus*.

What is the position of those genera of the Cheloneae which are characterized by loculicidal dehiscence of the capsule? Pennell (1935) apparently considered them to be closely related to genera of another tribe. Unfortunately, he was no more specific than this.

Can the presence or absence of staminodes be used as an important characteristic in the redefinition of the Cheloneae? As this tribe is currently defined, it includes genera which possess staminodes and those which do not. Polak (1900) showed that most Cheloneae possess one or more staminodes and suggested an investigation of the systematic position of those genera which do not. It is important to realize in connection with the evaluation of the importance, in the Cheloneae, of the presence or absence of staminodes that at least one genus of this tribe, *Scrophularia*, most of whose species have staminodes, contains several species in which the staminode is completely lacking (Stiefelhagen, 1910). This is in contrast to those genera, e.g., *Penstemon* and *Chelone*, which are characterized by the constant presence of staminodes.

The systematic position of *Scrophularia* needs further investigation. The seeds of this genus are, in their gross external and internal structure, almost identical with those of *Verbascum* and *Celsia*. The microscopic structure of the testae of *Scrophularia* and *Verbascum* is "ganz

analog" (Bachmann, 1882). Schmid (1906) asserted that *Scrophularia* and *Verbascum* are obviously more closely related to each other than current systems indicate. He found the development of the endosperm and haustoria and the behavior of the tapetal layer to be very similar in these two genera. Hartl (1959) discussed structural resemblances among the seeds of *Scrophularia*, *Verbascum*, *Celsia*, and *Sutera* and designated the seeds of these taxa as the "Scrophularia-type." He concluded that "Gattungen mit Samen vom Scrophularia-Typ scheinen untereinander taxonomisch verwandt zu sein." Other points of resemblance of *Scrophularia* to *Verbascum* and *Celsia* are its sometimes hairy filaments, its reniform anthers with wholly confluent sacs, and its septicidal, many-seeded capsule. The inflorescence of certain species of *Scrophularia* (e.g., *S. vernalis*) bears a great resemblance to that of certain *Verbascum* species (e.g., *V. lychnitis*). *Scrophularia laciniata*, *S. canina*, *S. hoopii*, and other species of the genus have lacinate leaves, a characteristic, not at all common in the Scrophulariaceae, possessed also by certain *Celsia* species (e.g., *C. orientalis*). It is interesting that in the *Genera Plantarum* of Endlicher (1836-40) the genus *Scrophularia* is included with *Verbascum* in the Verbasceae.

What is the taxonomic significance of the distinct stigmas of *Dermatocalyx* and *Uroskinnera*? Other genera of the Cheloneae sensu Wettstein possessing this characteristic must, as shown previously, pass to the Gratioleae. Study of *Dermatocalyx* and *Uroskinnera* may show that they, too, must be transferred from the Cheloneae. Unfortunately, Schultes (1941), in his synopsis of *Uroskinnera*, failed to consider the systematic position of the genus.

The systematic position of *Paulownia tomentosa* is as yet undetermined. This species, named *Bignonia tomentosa* in 1784, was renamed *Paulownia tomentosa* by Siebold and Zuccarini in 1835 (*fide* Campbell, 1930). Endlicher (1836-40) transferred it from the Bignoniaceae to the Scrophulariaceae because of the presence of endosperm in its seeds. This character, according to Campbell (1930), is the only one by which it differs from typical members of the Bignoniaceae. In the mature seed are found two or three layers of endosperm cells (Millsaps, 1936). *Paulownia* is included in the Scrophulariaceae in *Die Natürlichen Pflanzenfamilien* (Wettstein, 1891). However, the genus was referred to the Bignoniaceae by Hallier (1903) and, later, by Campbell (1930) and Li (1947). Pennell apparently was in agreement with this transfer (*fide* Britton, 1920). Nevertheless, in the eighth edition of *Gray's Manual of Botany* (Fernald, 1950) and the *New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada* (Gleason, 1952), *Paulownia* is found among the Scrophulariaceae. Of the genus Gleason (Gleason, 1952) wrote: "The structure of the placenta and the capsule and the presence of endosperm confirm its presence in the Scrophulariaceae." (Placental differences between the Scrophulariaceae and the

Bignoniaceae were pointed out by Bureau, 1863.) Steenis (1949) advocated the inclusion of *Paulownia* (and *Wightia*) in the Scrophulariaceae.

A solution to the problem of the position of *Paulownia* will never be reached by transferring the genus back and forth between the Bignoniaceae and the Scrophulariaceae. What is needed is a detailed study of the seeds of the Bignoniaceae to determine if the absence of endosperm is constant in this family. Following this, a comparative study of the placentae of the Scrophulariaceae and the Bignoniaceae would reveal if the differences reported by Bureau are constant. Then, and only then, may *Paulownia* be placed with certainty.

GRATIOLEAE

As outlined by Bentham (1846) as Gratioleae, subtribe Eugratioleae, and as summarized as Gratioleae by Wettstein (1891), this taxon comprises a large assemblage of obviously related genera (with the exceptions noted below). The tribe is characterized by a uniformity of seed types that is found in no other tribe of the Scrophulariaceae. Most of the genera of the Gratioleae whose seeds I have studied are characterized by either scalariform-reticulate (*Bacopa* type) or sulcate scalariform-reticulate, small (less than 0.7 mm in length), numerous seeds. However, pitted seeds occur in *Lindernia* and *Torenia*, and furrowed seeds in *Schistophragma* and *Stemodia*. (See Thieret, 1954, for illustrations of several seed types of the Gratioleae.) The Gratioleae are further distinguished by usually distinct stigmas, a feature found only rarely in the rest of the Antirrhinoideae.

To the genera included by Wettstein in the Gratioleae must be added *Leucocarpus*, *Hemichaena*, and *Berendtia* from the Cheloneae *sensu* Wettstein. These genera, as previously discussed, possess a combination of characters which shows them to be allies of *Mimulus*. *Scoparia* and *Capraria*, placed in the Digitaleae by Bentham and retained there by Wettstein although the exterior posterior corolla lobes of these genera exclude them from the Rhinanthoideae, must be transferred to the Gratioleae as evidenced by their frequently four-angled stems, their delicate, relatively long pedicels, their axillary flowers, and especially by their possession of glands on the calyx, pedicel, etc. (for a discussion of these glands see Solereder, 1899) (Pennell, 1935). The small, globose, 4-valved capsules of *Scoparia* and *Capraria* resemble those of *Conobea* Aubl. and many other Gratioleae. The seeds of these two genera are of the *Bacopa* type characteristic of many Gratioleae.

Two genera, *Monttea* and *Melosperma*, included in the Gratioleae by Wettstein, are surely out of place in this tribe. In the case of *Melosperma*, its few large seeds and spatulate embryos seem to exclude it from a tribe characterized otherwise by numerous small seeds and terete embryos. According to Reiche (1911), the bilocular ovary of *Melosperma andicola* (the only known species) contains many ovules in each locule. At maturity, however, the capsule contains only a few

(6-8) seeds with but little endosperm. The stigmas of *Melosperma* are united, another indication that it should be removed from the Gratioleae.

In the case of *Monttea*, Reiche (1911) described the ovary as containing many ovules but the capsule as containing only one or two large seeds. The seeds apparently are without endosperm (Bureau, 1863; Weberbauer, 1901). As in *Melosperma*, the stigmas are united.

The systematic position of *Melosperma* is difficult to ascertain. Certainly it is out of place in any of the tribes of the Antirrhinoideae as now defined (including the extremely ill-defined Cheloneae *sensu* Wettstein). *Monttea* is also difficult to place in any of the existing tribes of the Scrophulariaceae. Bureau (1863) suggested that this genus (and *Oxycladus*, included by Wettstein in *Monttea*) be segregated as a new tribe.

After a study of the aestivation of the corolla, the stamens, and other characteristics of a number of Indian species of *Lindenbergia* and related genera, Brühl (1920; abstract in Dudgeon, 1920) assigned the genus to the Rhinanthoideae either near *Euphrasia* or near the head of the sub-family since it appeared to him to be a connecting link with the Gratioleae of the Antirrhinoideae with which it has usually been placed. *Lindenbergia* has recently been studied by Hartl (1957), who referred it to the Gratioleae.

The genus *Conobea* (*sensu* Wettstein, 1891) is manifestly a heterogeneous assemblage of plants. This fact is revealed especially by an examination of the seeds of the genus. The seeds of section *Sphaerotherca* are scalariform-reticulate; those of the three species of section *Leucospora* are scalariform-reticulate, sulcate scalariform-reticulate, or spirally furrowed, respectively; and those of section *Schistophragma* are spirally furrowed. A natural treatment of this aggregate would give generic status to each of these sections after revising each of them.

The revised section *Sphaerotherca* (*Conobea* Aubl.) would contain the three species therein included by Wettstein and, in addition, *Conobea vandellioides* Benth. from section *Leucospora*. From the latter section *C. intermedia* must be transferred to section *Schistophragma*, thus leaving section *Leucospora* with but one species, *C. multifida* (Michx.) Benth. Section *Schistophragma*, then, would contain *C. intermedia* Gray in addition to *C. pusilla* Benth. Each of these sections must now be raised to generic level as *Conobea* Aubl., *Leucospora* Nutt., and *Schistophragma* Benth.

Leucospora multifida (Michx.) Nutt., originally *Capraria multifida* Michx., was made the type of the new genus *Leucospora* by Nuttall. In Bentham's revision of 1846 it was included as a member of *Conobea* Aubl. of lowland northern South America and has since been usually treated as such. Actually, it has little in common with this genus of tropical America.

Schistophragma Benth. was based on *S. pusilla* Benth. ranging from

northern Colombia northward to Mexico. Later, *S. pusilla* was included in *Conobea* Aubl. by Bentham and Hooker (1876), a transfer which probably would not have been made had the authors taken into account the morphology of the seeds. *Conobea intermedia*, of northwestern Mexico and the adjacent parts of New Mexico and Arizona, was described by Gray. This species must now be transferred to *Schistophragma*, a distinctive genus characterized principally by spirally furrowed seeds, pinnatifid leaves, and elongate to linear capsules.

The genera *Conobea*, *Schistophragma*, and *Leucospora* may be distinguished as follows;

Seeds scalariform-reticulate, in more than one row within each valve of the capsule; capsule depressed globose; leaves serrate, glandular-punctate; plant glabrous; stem quadrangular; pedicels bibracteolate; posterior lip of corolla shorter than anterior lip; connective not enlarged, anther cells proximate *Conobea*

Seeds sulcate scalariform-reticulate, in more than one row within each valve of the capsule; capsule ovoid; leaves pinnatifid, not punctate; plant pubescent; stem terete; pedicels not bibracteolate; corolla lips of equal length; connective slightly enlarged, holding the cells of the anther somewhat apart *Leucospora*

Seeds spirally furrowed, in one row within each valve of the capsule; capsule elongate to linear; leaves pinnatifid, not punctate; plant pubescent; stem quadrangular; pedicels bibracteolate; corolla lips of equal length; connective slightly enlarged, holding the anther cells somewhat apart *Schistophragma*

These three genera are certainly not so closely related as their inclusion as sections in *Conobea* (*sensu* Wettstein) would indicate. *Conobea* Aubl. is apparently a relatively unmodified member of the Gratioleae by virtue of its scalariform-reticulate seeds, globose capsules, and serrate leaves. *Leucospora* seems somewhat isolated from other Gratioleae, its seeds separating it from *Schistophragma* with which it agrees in habit and pinnatifid leaves, and its stamens with parallel anthers separating it from *Micranthemum*, *Lindernia*, *Hemianthus*, and *Limosella* with which it agrees in seeds. The relationships of *Schistophragma*, on the other hand, appear to be easier to establish. The distinctive markings of its seeds, which Pennell (1940) called apparently "unique in the Scrophulariaceae," do not, however, occur only in this genus but also in *Stemodia*. Another point of agreement between these two genera is seen in the slightly enlarged connective holding apart the cells of the anthers of both genera. So close are *Schistophragma* and *Stemodia* that a suffrutescent form of *Schistophragma intermedia* from Lower California was described by Brandegee as *Stemodia polystachya*. This name should probably be reduced to synonymy under *Schistophragma intermedia*, although further study may indicate that the lower California suffrutescent form of the species be given sub-specific or even specific rank.

The genus *Lindernia* is characterized by two types of seeds: (a) sulcate scalariform-reticulate (e.g., in *L. dubia* and *L. anagallidea*), and (b) pitted (in two species, *L. crustacea* and *L. diffusa*). Pitted seeds of similar aspect occur in at least those species of *Torenia* examined by me. Seeds of this type, in the Scrophulariaceae, I have seen only in *Torenia* and the above-mentioned species of *Lindernia*, suggesting that a study of these genera with a view to their revision is necessary. This suggestion is confirmed by a review of the history of the widespread plant currently known as *Lindernia crustacea*. Originally described by Linnaeus as *Capraria crustacea*, it was transferred by Chamisso and Schlechtendal to *Torenia*. Finally, it was placed in *Lindernia* by Mueller (*fide* Pennell, 1920). In his "Scrophulariaceae of Colombia" Pennell (1920) advocated the alliance of this species with *Torenia*; 15 years later, however, he treated it as *Lindernia crustacea* (Pennell, 1935). Here, then, is a plant which has been placed both in *Torenia* and *Lindernia*, suggesting, of course, that it combines the characteristics of both genera. It has the pitted seeds characteristic of apparently only one other species of *Lindernia*, but, in contrast, characteristic of a number of species of *Torenia*. It seems quite possible that a detailed study of these genera will indicate that they should be combined. That they are closely related has long been recognized. In at least one other instance in the Gratioleae, the union of groups previously given generic rank has resulted in the formation of a larger but more natural genus. This case is that of *Lindernia* itself. As now recognized (Mukerjee, 1945; Pennell, 1935), *Lindernia* has been enlarged to embrace *Vandellia*, *Ilysanthes*, and *Bonnaya*.

SELAGINEAE

The tribe Selagineae consists of about 120 species of herbaceous or shrubby plants of healthlike appearance, principally South African but occurring also in Madagascar and on the mountains of tropical Africa (Rendle, 1925).

The Selagineae, long given family status, were first reduced to tribal rank in the Scrophulariaceae by Baillon (1888), whose treatment of them was accepted by Wettstein (1891) and Hallier (1903). Previous to (and even since) Baillon's work, the Selagineae were (and have been) regarded as a distinct family related either to the Myoporaceae and Verbenaceae (Bentham and Hooker, 1876; Choisy, 1848; Endlicher, 1836-40; Hutchinson, 1926; Rolfe, 1883; Van Tieghem, 1891) or to the Scrophulariaceae (Marloth, 1932; Rendle, 1925).

In the majority of these interpretations the Selaginaceae comprise those genera included in the Selagineae (*sensu* Wettstein, 1891) and, in addition, the genus *Lagotis*. Van Tieghem (1891), however, enlarged the Selaginaceae to include the Myoporaceae and Globulariaceae, thus distinguishing three tribes as follows: Myoporeae ("Etamines á quatre sacs, carpelles fermés"), Selagineae ("Etamines á deux sacs, carpelles

fermés”), and Globularieae (“Étamines á quatre sacs, carpelles ouverts”).

The plan of structure of the flowers of the Selagineae (*sensu* Wettstein) is that of the Scrophulariaceae. The basis for their uncertain systematic position is found in the structure of the ovary, which contains in each cell a single pendulous ovule, and of the fruit, a schizocarp which consists of two equal or unequal cocci which become free when mature, each of these containing a single seed. Choisy (1848) regarded the Selaginaceae as being related to the Verbenaceae and the majority of labiates on the basis of the structure of the fruit. He noted, however, that this family differs from these taxa by the presence of endosperm (according to Martin, 1946, certain verbenaceous and labiate genera possess an endosperm), by the position of the embryo in the seed (the radicle is superior in Selaginaceae but inferior in Verbenaceae), by the frequently alternate leaves, and by other minor characters.

The most critical discussion of the systematic position of the Selagineae is that given by Hallier (1903) who, after a study of numerous specimens of members of this taxon, was in complete agreement with its reduction, by Baillon and Wettstein, to tribal rank in the Scrophulariaceae.

The presence of a schizocarp need not exclude the Selagineae from the Scrophulariaceae for this type of fruit is also present in the genus *Lagotis*, belonging to the Veroniceae (Hallier, 1903; Pennell, 1933; Thieret, 1955). After studying the anatomy of the fruits of the Scrophulariaceae, Weberbauer (1901) commented on the Selagineae: “Ich [konnte] mich nicht entschliessen, die Gruppe der Selagineae, welche unter den Scrophulariaceen ziemlich scharf abgesondert besteht, und der früher der systematische Rang einer Familie zuerkannt wurde, auf Grund der Frucht-Anatomie zu zersplittern.”

ANTIRRHINEAE

In Wettstein's revision of the Scrophulariaceae the Antirrhineae are placed centrally in the Antirrhinoideae. This tribe, however, surely is one of the most highly evolved of all Scrophulariaceae as is evidenced by the elaborate and specialized seeds, the extreme zygomorphy of the corolla, the greatly modified dehiscence of the capsule, and the alternate or scattered phyllotaxy. The Antirrhineae, thus, seem more naturally placed as the most advanced tribe in the antirrhinoid division of the family.

The tribe, as defined by Wettstein, includes three genera with septicidal capsules. These taxa, *Nemesia*, *Diclis*, and *Colpias*, were transferred to the Hemimerideae by Diels (1897). Rothmaler (1943), whose synopsis of the Antirrhineae is the only one since that of Wettstein, also referred these genera to the Hemimerideae. Thus, with the removal of *Nemesia*, *Diclis*, and *Colpias*, the Antirrhineae become a tribe uniformly characterized by loculicidal transverse or poroid ruptures of the capsule.

DIGITALEAE

The tribe Digitaleae as presented by Wettstein (1891) is probably the least coherent in his revision of the Scrophulariaceae. Referring to Wettstein's key to the tribes of the family, one may note that all members of the Digitaleae, as there indicated, should have at least two characteristics in common: the upper corolla lobes internal in the bud, and plants not parasitic. All the genera in Wettstein's Digitaleae (except *Scoparia* and *Capraria*, since transferred to the Gratioleae) apparently possess these features; however, the following key to the genera *Digitalis* and *Veronica* will emphasize the heterogeneity, in other features, found in the Digitaleae.

stigmas distinct; anther cells divaricate; capsule woody, septicidal	<i>Digitalis</i>
stigmas united; anther cells parallel; capsule hardly or not woody,		
loculicidal	<i>Veronica</i>

Thus, as in the case of Cheloneae sensu Wettstein, the Digitaleae sensu Wettstein comprise genera which should not be included in the same tribe if that tribe is to be homogeneous. It is unfortunate that Wettstein did not follow Bentham (1846) who placed *Veronica* and *Digitalis* in the separate tribes Veroniceae and Digitaleae. The splitting of Wettstein's Digitaleae into at least two tribes has been regarded as necessary by Rouy (1909) and Pennell (1921).

Further study is necessary before final conclusions may be reached in regard to the dismemberment of the Digitaleae. However, discussion of the steps already taken to revise the Digitaleae seem pertinent here.

According to Pennell (1935), most of the genera in Wettstein's Digitaleae pertain to the Veroniceae "as now understood." Pennell, however, failed to clarify what seems to be an important point, i.e., the current understanding of the Veroniceae. In his discussion of the Digitaleae he stated that this tribe is a small one, comprising only the genus *Digitalis* and perhaps *Rehmannia*. (Many years before, *Rehmannia* had been broken up into three genera by Solereder, 1909, and two of these, including *Rehmannia* proper, had been transferred to the Gesneriaceae; even earlier, Hallier, 1903, suggested that *Rehmannia* is gesneriaceous; in contrast, see Burt, 1954, for the suggestion that *Rehmannia* has, to the student of Gesneriaceae an "alien look.")

Certain genera of the Digitaleae sensu Wettstein (and even sensu Bentham) belong clearly to the Veroniceae emend., as pointed out by Pennell (1921, 1933, 1937). These are *Veronica*, *Veronicastrum*, *Hebe*, *Picrorhiza*, *Wulfenia*, *Synthyris*, *Besseyia*, and *Aragoa*. Pennell (1933) included in the Veroniceae emend. also the genus *Lagotis*, a taxon whose affinities, as will be shown later, have been much discussed. To these genera I would follow Van Tieghem (1891) and add *Globularia*, which has traditionally been placed in the Globulariaceae (Thieret, 1955).

In addition to those listed above, two additional genera with New World representatives are included in Wettstein's Digitaleae. The af-

finities of the genus *Sibthorpia*, recently monographed by Hedberg (1955), are presently not clear. Pennell, in limiting the Digitaleae emend. to *Digitalis* and perhaps *Rehmannia*, apparently excluded *Sibthorpia* from this tribe. On the other hand, *Sibthorpia* was implicitly excluded from the Veroniceae emend. by Pennell (1937) when he referred to *Aragoa* as the only genus of this alliance native to tropical America (*Sibthorpia* is native in tropical America as well as in Africa and Eurasia, according to Hedberg, 1955).

The genus *Ourisia*, with members in South America, Australia, and New Zealand, combines the united stigmas of the Veroniceae emend. with the divaricate anther cells of the Digitaleae emend. Only future study can decide the affinities of *Ourisia*, although Hallier (1903) advocated transferring certain species of this genus to the Gesneriaceae.

Floral and vegetative features of the genus *Lagotis* (*Gymnandra*), comprising 13 species (Li, 1954) ranging from the highlands of Asia Minor through central Asia to subarctic Alaska and the Yukon, prove it an ally of *Picrorhiza*, *Wulfenia*, *Synthyris*, *Besseya*, and *Globularia* (Hallier, 1903; Pennell, 1933; Thieret, 1955). Its fruit, however, is schizocarpic, being sometimes separable into two indehiscent, one-seeded cocci. (According to Pennell, the fruit is a capsule. It is not.) Thus, the fruit of *Lagotis* is essentially similar in type to that of the Selagineae; in cellular structure, however, it appears to be similar to the fruit of *Aptosimum* and *Monttea* rather than that of the Selagineae (Weberbauer, 1901).

The genus *Lagotis* was founded by Gaertner in 1770 on a plant from Kamchatka described by Gmelin in 1768 as a *Veronica*. Until 1846 the genus was treated as a close ally of *Veronica* (e.g., Endlicher, 1836-40). In that year, however, Bentham (1846) excluded *Lagotis* from the Scrophulariaceae and referred it, though with uncertainty, to the Selaginaceae on the basis of the structure of its fruit. Choisy (1848), in his monograph of the Selaginaceae, wrote that an affinity of *Lagotis* with this family on the basis of fruit structure is not to be denied but that most of the floral characters (e.g., distinctly bilabiate corolla, capitate stigma) of *Lagotis*, as well as its habit and distinct geographical distribution, indicate the contrary. In Choisy's opinion the assignment of *Lagotis* to the Selaginaceae appears to be less natural than its assignment as a near ally of *Veronica*. Nevertheless, it was treated under the Selaginaceae by Choisy and by many subsequent authors (Bentham and Hooker, 1876; Gray, 1886; Hooker, 1885; Printz, 1921; Rolfe, 1883; Van Tieghem, 1891). In his *Histoire des Plantes*, Baillon (1888) restored *Lagotis* to its position in the Digitaleae near *Veronica*. In this he was followed by Wettstein (1891) in *Die Natürlichen Pflanzenfamilien*. This transfer was at first opposed by Hallier (1901) but subsequently accepted and defended by him (1903). Indeed, Hallier's discussion of the systematic position of *Lagotis* is the most critical and detailed in print. He referred to *Lagotis* as ". . . nichts anderes, als eine im Fruchtknoten

und der Zahl der Samenknospen stark reduzierte, im Uebrigen nur noch durch grössere Brakteen ausgezeichnete Sektion von *Wulfenia*." Of the long accepted alliance of *Lagotis* with the Selagineae he stated: "In Tracht und geographischer Verbreitung ist *Lagotis* von den eigentlichen Selagineen grundverschieden; das wenige, was sie mit ihnen gemein hat, nämlich der in jedem Fach nur noch eine einzige hängende Samenknospe enthaltende Fruchtknoten, beruht wohl mehr auf einer parallelen, auf gleicher Stufe angelangten Reduktion, als auf engerer Verwandtschaft." Since *Lagotis* was included in the Digitaleae sensu Wettstein, it has been treated as a *Veronica* ally by most authors.

Apparently previously unobserved or unreported is an interesting feature of the genus *Lagotis*; the posterior lobes of the corolla are external in the bud. This characteristic, if the relative position of the corolla lobes in aestivation be used as the basis upon which to define the subfamilies of the Scrophulariaceae, would exclude *Lagotis* from the Rhinanthoideae, the sub-family wherein are found *Veronica* and allies. Since *Lagotis* is surely an ally of *Veronica*, as Hallier so clearly demonstrated, aestivation characteristics in this case seem to be of little importance in establishing relationships (compare Diels, 1897, and Hartl, 1955).

Now that we have reviewed some of the major taxonomic problems in the Scrophulariaceae—and some of the major changes made in the classification of the family since Wettstein's revision of it—we may well ask ourselves, "What does all this mean?" Obviously, the most important fact gleaned from such a review is that the Scrophulariaceae, generally considered such a "well-known" family, are far from being "well-known." A satisfactory tribal classification of the family has not yet been attained; even the limits of the family are not agreed upon. Next we might ask ourselves, "Where do we go from here?" The course, to me at least, is clear. A world monograph of the Scrophulariaceae on the generic level, making use of all available collections and all techniques available to the modern taxonomist, should provide the data prerequisite to a logical treatment of the family. Most of today's taxonomists are so concerned with studies of genera or of floras of limited areas that the larger problems—such as supra-specific classification of the Scrophulariaceae—are neglected. Such neglect is, of course, understandable when one realizes that the neglected problems are often those whose study requires the assembling of a vast amount of herbarium material from the world over. Such assemblage has its own problems of expense, storage, etc., that perhaps few herbaria and taxonomists are able to cope with. Nevertheless, the collections for such studies are available; perhaps someday someone will conceive of a way to use them. (see Just, 1953, for an able discussion that is applicable here.) It should be apparent to all that, in the Scrophulariaceae at least, the work of the taxonomist has just begun.

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